Apertural Barriers in Pacific Island Land Snails of the Families Endodontidae and Charopidae

BY

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(7 Plates)

More than 140 years ago Guilding (1829: 168) speculated that the barriers found in the apertures of many land snails serve to lessen predation by arthropods. Comparatively little data has accumulated since then concerning barrier microstructure and patterns of growth. Solem (1972) briefly reviewed patterns of barrier formation, demonstrated that the barriers have weak to prominent microsculpture, and hypothesized that the pointed denticles found on the surface of many barriers evolved from a primitive, very widely distributed apertural microsculpture. This consists of platelets whose raised edges face the outer plane of the aperture, while their upper surface slopes gradually backwards to merge with the smooth surface of the inner lip and wall edges. When the aperture of the shell is greatly constricted by barriers, as in the polygyrid *Stenotrema* (Solem, 1972: figs. 23–24), the platelets are proportionately larger than in species that lack these barriers. The function of these platelets may be to aid the animal in extending its body after being retracted. The minute platelets would provide a roughened surface for the mantle edge to grip and hence help the snail obtain purchase for forward movement of the mantle collar from deeply recessed within the aperture to its typical position covering most of the parietal, columellar and palatal lips.

This report is concerned with patterns of denticle structure on apertural barriers in the Pacific Island land snail families Endodontidae and Charopidae. Prior to reviewing the anatomy of these groups, species with such barriers were placed in the genus *Endodonta* and species lacking such barriers in the genus *Charopa*. Barriers occur in both families and the traditional generic limits are totally incorrect. Data concerning the shell sculpture and anatomical differences between these groups will be given elsewhere (Solem, in press). The microarmature on the barriers is shown to characterize the two families just as strongly as do the anatomical or sculptural features.

Explanation of Figures *1* to *6*

Species studied (arrows indicating barriers shown on subsequent plates)

Figure *1*: Undescribed genus and species from Rapa, Austral Islands

Figure *2*: *Thaumatodon* spec. nov. from Eua Island, Tonga

Figure *3*: *Endodonta fricki* (Pfeiffer, 1858) from Waianae Mountains, Oahu, Hawaii

Figure *4*: "*Endodonta*" *callizonus* (Möllendorff, 1900) from Ponape, Caroline Islands

Figure *5*: Undescribed genus and species from Peleliu, Palau Islands

Figure *6*: "*Endodonta*" *graeffei* Mousson, 1869 from Upolu, Western Samoa

Scale lines equal 1 mm

Explanation of Figures *7* to *10*

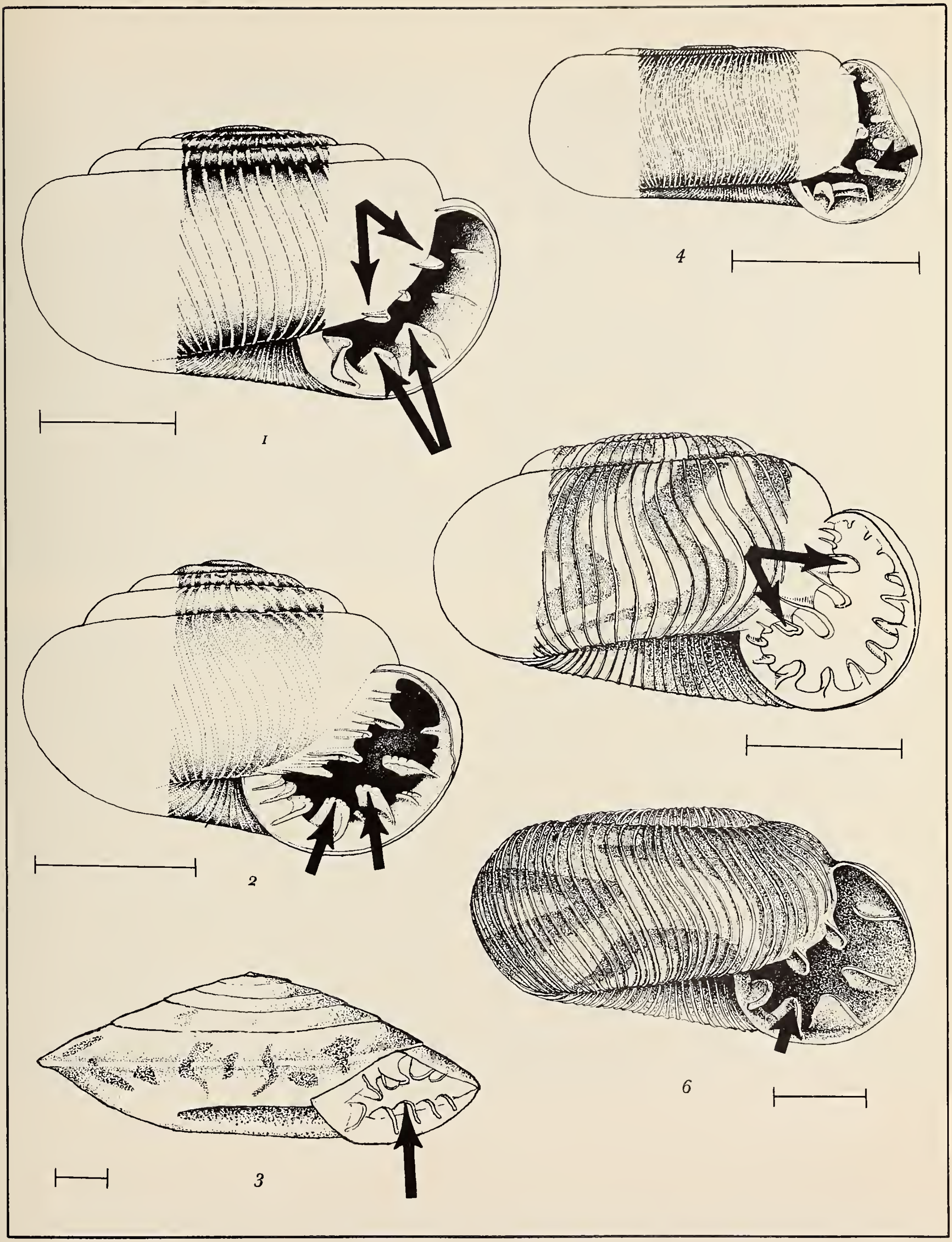
Apertural barriers in species from Rapa Island

Figure *7*: Anterior ends of 2nd and 3rd parietal barriers and portion of 1st parietal ×308

Figure *8*: Upper edge of 1st parietal barrier showing denticulated posterior portion ×937

Figure *9*: Detail of denticulated portion on 1st parietal barrier showing variation in denticle form ×3070

Figure *10*: Posterior margin of 1st and 2nd palatal lamellae showing limited portion of barrier on which denticles are present ×298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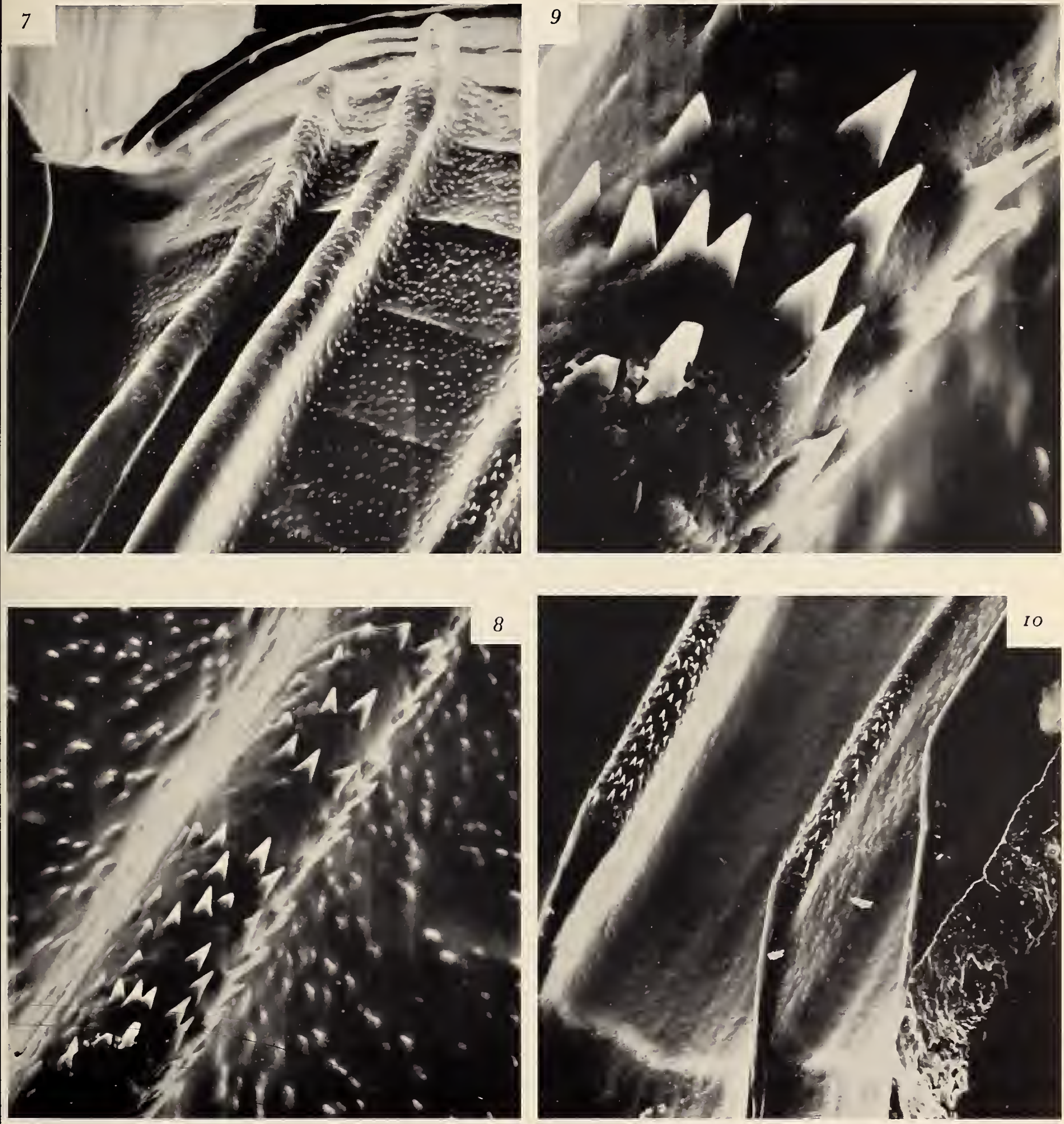
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ACKNOWLEDGMENTS

Scanning electron microscope photographs illustrating this paper were taken with a Cambridge Mark I stereoscan at Alpha Research and Development Company in Blue Island, Illinois. I am deeply indebted to Mr. John Brown and his staff for their skilled operation of the microscope, to Fred Huysmans of Field Museum for his care in preparing prints, to Margaret Ann Moran, Jane Calvin and Sander Heilig for line drawings, and to both Field Museum and the National Science Foundation (GB-6779) for funding this research. The photographs were prepared some time ago, but publication has been withheld until exploratory work on apertural barriers in other families (Solem, 1972) could be completed and thus provide background data for understanding the significance of these microstructures.

PREVALENCE and GROWTH of BARRIERS

Species of both the Charopidae and Endodontidae have apertural barriers (Figures *1* to *6*), but the proportion of species with and without such barriers varies between the two families. Summarizing data from monographs of these groups (Solem, in press), the percentage of species level taxa with barriers is:

	Parietal barriers	Palatal barriers
Endodontidae	99.5% (of 185)	88.6%
Charopidae	32.6% (of 95)	28.4%

While the absence of apertural barriers would be highly suggestive that the unknown species belongs to the Charopidae, possession of such barriers gives no clue as to family unit. The only species of Endodontidae that completely lacks the barriers, *Nesodiscus fabrefactus* (Pease, 1864), has one race (*piceus*, Garrett, 1884) that retains traces of these barriers. Their absence is a secondary loss. Reduction in number and size of the barriers correlates, in general, with increasing shell size. In both families the barriers are present throughout the independent life of the snail. Hatchlings show a partial to complete set of barriers just inside the shell aperture. In some species the number of parietal or palatal barriers will increase from juvenile to adult. Barriers can extend posteriorly one-sixteenth to more than an entire whorl, depending on the species.

As the shell grows, the barriers are added to at the anterior margin and resorbed posteriorly. This is not a continuous process, since SEM examination of the resorption surface shows a layered pattern consistent with interrupted accretion (Solem, unpublished). Within a species population, the exact length of the barriers varies slightly from individual to individual, which also is consistent with a surge of posterior resorption alternating with a surge of anterior incremental growth. Through repeated alternations of growth and resorption the position of the barriers relative to the apertural lip remains virtually constant and the calcium investment in barrier formation remains stable. If an amount of calcium withdrawn from the posterior portion of the barriers is then deposited anteriorly, no or very little additional calcium must be extracted from the environment. If anterior deposition preceded posterior resorption, then an extra quantity of calcium would have to be first extracted, then deposited, resorbed posteriorly and stored in mantle tissue until the next growth surge. This would be far less efficient in terms of energy budget for the snail.

FORM and NUMBER of BARRIERS

At the optical level of study, size, position, number and shape of the barriers are very useful identification features. Often these details provide the easiest and quickest means of identifying sympatric species that are similar in shell size and shape. The differences between the species shown in Figures *1* to *6* are typical. This is not to be taken as indicating there is no intraspecific variation. Several endodontid species are known where the number of parietal barriers is either 3 or 4, with the ratios suggesting that simple Mendelian dominance controls the variation. One endodontid species from Rapa Island can have 0, 1, 2, 3, 4, or 5 palatal barriers, while a charopid from Guam has from 4 to 8 palatal barriers. These are extreme examples, with most species showing relatively trivial variation in barrier size and shape.

In general, most barriers are simple ridges. They are largest in size on the lower parietal and lower palatal walls. Some barriers may become sinuately twisted in adult specimens (see columellar barrier in Figure *1*), but most retain a ridgelike or semicircular profile. Quite frequently the parietal and palatal barriers will almost touch in the middle of the aperture. In some cases there even may be overlapping interdigitation of the barriers with the lower parietal, for example, extending to a point that it cuts the plane drawn between the upper edges of the two opposite palatal lamellae. The illustrated species have less highly developed barriers, but their pattern is essentially the same. Almost without exception, the upper parietal-palatal region of the aperture will have very small barriers with a clear open area leading to the shell interior. It is through this passage that the bulky foot and buccal mass must be withdrawn and extended. In the basal and middle regions of the aperture, the degree of narrowing by the barriers frequently is so great that there is insufficient room for either the foot or buccal mass to pass.

MICROARMATURE ON BARRIERS IN THE ENDODONTIDAE

Figures *1* to *3* illustrate the shells of three species belonging to different lineages in the family, while Figures *7* to *13* and *23* and *24* are scanning microscope photographs of the particular barrier edges indicated by the black arrows in Figures *1* to *3*. The undescribed species from Rapa Island (Figure *1*) is moderately specialized in terms of genitalia and belongs to the most diverse genus living on that island. Its barrier structure is typical of the more generalized Endodontidae. A low angled view of the parietal wall looking from inside the aperture (Figure 7) shows the anterior ends of the 2nd and 3rd parietals, plus a small section of the 1st parietal barrier (lower right margin of photograph). The pattern of a callus being deposited over the ribbed surface of the preceding whorl and the irregularly pustulose surface of the callus is quite clear. These pustulations are the primitive microarmature found on the parietal and columellar wall of many snails. Figure *10* shows the posterior margins of the 1st and 2nd palatal barriers. This demonstrates that the minute denticulations are restricted to the upper edge and posterior end of the barriers. Figures *8* and *9* show higher magnification details of the denticulated section on the 1st parietal barrier. On both parietal and palatal barriers the denticles are triangular and point towards the outside of the aperture. The exact form of the denticles can be observed on the sides of the barriers in Figures *8* and *9*. It must be emphasized that these denticles are additive elements to the barrier surface. That is, they are separate elements from the normal surface of the barrier. This is quite unlike the situation in *Ptychodon microundulata* (Suter, 1890) (Solem, 1970: plt. 60, figs. 13–15) where the denticles are surface layer crystals that are greatly enlarged and extended.

Thaumatodon (Figure *2*) is a genus from western Polynesia, with its center of diversity in the Lau Archipelago of Fiji. Other species are known from Ellice, Cook, Samoa and Tonga. Derivative genera are found in Lau and the Palau group. This complex of genera is distinguished anatomically by a major alteration in the terminal male genitalia, and conchologically by the development of small "beaded" sculpture on the surface of all major and some minor barriers. This is the most strongly differentiated group of genera in the family. High magnification observation of the barriers (Figures *11* to *13*) in *Thaumatodon hystricelloides* (Mousson, 1865) from Western Samoa shows that denticulations are restricted to the raised beads (Figure *11*). These denticles are the same triangular additive points seen in the more generalized taxa. In this species the tips of the points are subject to great variation. A tendency towards blunting is evident. The lower part of Figure *11* shows the posterior resorption edge of the palatal barriers. The layered nature of the callus is obvious, while the porous appearance at the angle between the resorption plane and the palatal surface is caused by the preliminary weak acid etching of the callus.

Endodonta fricki (Pfeiffer, 1858) (Figure *3*) from Oahu, Hawaii is the fourth largest species in the Endodontidae, averaging 9 mm in adult diameter. The barriers are massive and the form of the denticles (Figures *23, 24*) is slightly modified. Most denticles (Figure *23*) are broadly triangular, but in areas (Figure *24*) they have become flattened anteriorly and have a spade-like edge. The Hawaiian Endodontidae are anatomically conservative although showing rather large conchological variation. The form of these denticles is rather different from that seen in the other two illustrated genera. Whether this is correlated with the increased size of *Endodonta,* or represents a general pattern of divergence in the Hawaiian taxa is uncertain. The palatal barriers in *"Endodonta" nudus* Ancey, 1899 from Kaiwicki, Hilo, Hawaii (FMNH 90319) have the denticles on the upper edge of the barrier with spade-like anterior edge, although denticles on the lateral

Explanation of Figures *11* to *13*

Apertural barriers in *Thaumatodon hystricelloides* (Mousson, 1865) from Upolu, Western Samoa

Figure *11*: Posterior margin of 2nd (right) and 3rd (left) palatal barriers showing resorption face (bottom of photograph) and restriction of denticulations to the "beads" ×292

Figure *12*: Surface of one "bead" showing variation in shape and angulation of denticulations ×2880

Figure *13*: Individual denticles ×10400

Explanation of Figures *14* to *16*

Parietal barriers in undescribed snail from Peleliu, Palau Islands

Figure *14*: Parietal wall showing bifurcated 1st (left) and simple 2nd, 3rd, and 4th parietal barriers. ×140
Posterior margin at top of figure

Figure *15*: Upper edge of 3rd parietal barrier ×1185

Figure *16*: Detail of transverse plates on upper edge of barriers ×3315